

HIGH POLYPLOIDY AND THE ORIGIN OF BALSAMORHIZA MACROPHYLLA (COMPOSITAE)

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Balsamorhiza comprises about 12 species of perennial sunflowers native to the western and northwestern United States and adjacent parts of Canada. Strong morphological and ecological evidence suggests that when ecological barriers are broken between most species of *Balsamorhiza*, natural hybridization occurs (Maguire, 1942; Ownbey and Weber, 1943). *Balsamorhiza macrophylla* Nutt. is therefore unusual in being one of the few entities in the genus in which natural hybridization is unknown. Although the species is relatively uniform, it is intermediate in a number of characteristics between certain species pairs with which it is sympatric or nearly so.

Cytological examination has indicated that *B. macrophylla* is a high polyploid, with $n = 100 \pm 2$ (Table 1). Since related species all have $n = 19$ (Weber, 1946; and Table 1), *B. macrophylla* is so far known only as an approximate decaploid, with no intermediate ploidy levels recorded.

In this report the putative origin of *Balsamorhiza macrophylla* is discussed, as a basis for further investigations, in terms of the available karyological data and some morphological comparisons. These comparisons have been extended to the genus *Wyethia*, which is so closely related to *Balsamorhiza* that the distinction of the two genera has been questioned (Weber, 1946).

MATERIALS AND METHODS

Qualitative morphological comparisons were made from living material of *B. macrophylla* Nutt., *B. sagittata* (Pursh) Nutt., *B. hookeri* Nutt. vars. *hispidula* (Sharp) Cronq. and *idahoensis* (Sharp) Cronq. and *Wyethia amplexicaulis* Nutt. (Table 2). Field data include notes on occurrence in relation to plant association, soil type, elevation, and water regime, and were collected for all the above-mentioned taxa and for some putative hybrid populations. Limited breeding experiments have also been undertaken.

Cytological observations were made from squash preparations of meiotic pollen mother cells. Buds were fixed in ethanol:acetic acid (3:1), stored in 75% ethanol under refrigeration, squashed in 1% aceto carmine, and examined with phase contrast. Voucher specimens have been deposited in the Garrett Herbarium, University of Utah (UT).

TABLE 1. NEW CHROMOSOME NUMBERS IN BALSAMORHIZA

Species	Gametic number	Locality
<i>B. hookeri</i> var. <i>hispidula</i>	19,20 (fig. 1,2)	Mouth of Big Cottonwood Canyon, Salt Lake Co., Utah, <i>N. Helton</i> 5.
<i>B. hookeri</i> var. <i>idahoensis</i>	19	3 mi. n. of Sweet, Gem Co., Idaho, <i>N. Helton</i> 27.
<i>B. macrophylla</i>	100±2 (fig. 3)	Parleys Canyon at cutoff to East Canyon, Salt Lake Co., Utah, <i>N. Helton</i> 52.

OBSERVATIONS AND DISCUSSION

Chromosome numbers and meiotic behavior. Chromosome numbers of $n = 19$ have been reported for *B. sagittata*, *B. deltoidea*, *B. careyana*, *B. rosea*, *B. serrata* and *Wyethia amplexicaulis* by Weber (1946). In the present study chromosome numbers of $n = 19$ have been confirmed for *B. sagittata* and *W. amplexicaulis*, and for putative hybrids between *B. sagittata* and the two varieties of *B. hookeri*. New species records have been made for the two varieties of *B. hookeri* and for *B. macrophylla* (Table 1). The only exceptions to the number $n = 19$ were in one population of *B. hookeri* var. *hispidula* from which $n = 20$ was also recorded (figs. 1, 2), and in *B. macrophylla* from which the recorded number was $n = 100 \pm 2$ (fig. 3).

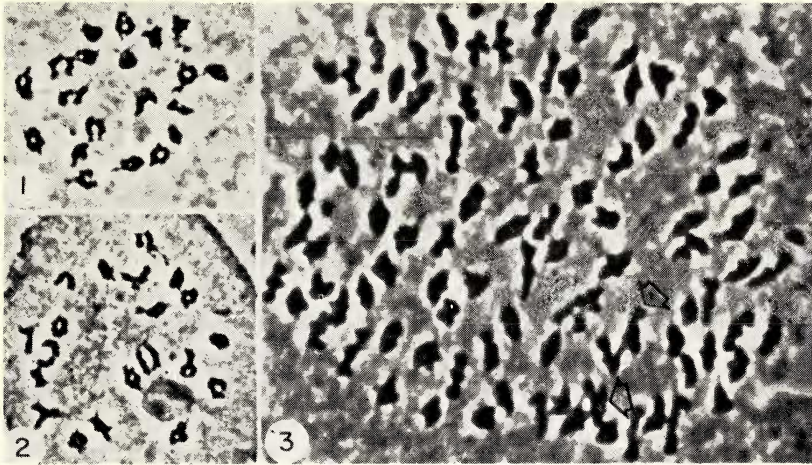
Balsamorhiza macrophylla is therefore approximately 10-ploid in relation to its congeners, and may be separated by a sharp karyological discontinuity. In the Compositae the only species known with chromosome numbers equalling or possibly exceeding that of *B. macrophylla* are three species of *Werneria* of the Peruvian highlands, with numbers of $2n = ca\ 206$ and $2n = ca\ 213$ (Diers, 1961).

Chromosome pairing behavior in the diploid taxa appeared to be normal, except for a low frequency of cells in populations of *B. hookeri* var. *hispidula*, in which anaphase bridges and lagging chromosomes were observed and also for some irregularity in some hybrid plants. Pairing behavior in *B. macrophylla* was highly regular (fig. 3), as most chromosomes were associated in normal bivalents, and maximum association observed was four quadrivalents. Diploidization is thus essentially complete in the materials examined.

Morphological comparisons. *Balsamorhiza* contains two sections, *Artorhiza* and *Balsamorhiza*, that are closely related but show some clear morphological differences. The two sections are also generally distinct ecologically (see below). Section *Artorhiza* is characterized by large, deep-seated caudices surmounted by multiple crowns, and the leaves generally have entire margins. Section *Balsamorhiza*, however, has much smaller caudices and often produces short, thick rhizomes that eventually produce separate rosettes, and mature plants have a simple crown bearing a single rosette of variously pinnatifid leaves.

TABLE 2. MORPHOLOGICAL CHARACTERISTICS IN BALSAMORHIZA AND WYETHIA

	<i>B. sagittata</i>	<i>B. hookeri</i> var. <i>hispidula</i>	<i>B. macrophylla</i>	<i>W. amplexicaulis</i>
Stem:				
length	2 to 6.5 dm	0.6 to 3 dm	3 to 10 dm	3 to 8 dm
vestiture	tomentose	pilose-hirsute, eglandular	pilose-glandular to glabrate	glabrate
Basal leaf:				
shape	deltoid	oblong-lanceolate	oblong-lanceolate	oblong-lanceolate
margin	entire	pinnately divided	pinnate or pinnately cleft	entire to denate
length	30 cm	10 to 40 cm	30 to 60 cm	20 to 40 cm
width	5 to 15 cm	c.5 to 15 cm	6 to 15 cm	5 to 15 cm
vestiture:				
abaxial	silvery tomentose	sparsely hispid, hispid-pilose	crisp hirsute to glabrous,	glabrous
adaxial	to velutinous	to hispidulose on margins	hirsute-ciliate on margins	glabrous
	cinereous-stigulose	globular-resinous hispid,	glandular, crisp hirsute	
		hispid-pilose to hispidulose	on veins, glabrous	
		on veins		
Phyllary:				
shape	ovate-lanceolate to lanceolate	linear to linear-lanceolate	lanceolate, oblong-lanceolate	ovate-lanceolate
apex	acuminate or attenuate	acute to acuminate	acute to acuminate	acute to acuminate
Ray:				
shape	oblong-lanceolate	not available	broadly oblong-elliptical	ovate-lanceolate
no. per head	mostly 13 to 21 (8 to 25)	10 to 16	8 to 16	6 to 16
length	2 to 4 cm	2.5 to 3 cm	3.5 to 5.5 cm	2.5 to 5 cm
Head:				
no. per peduncle	solitary or 2 or 3	solitary	solitary	several, occasionally solitary
diameter	6 to 8 cm	4.5 to 6 cm	8 to 12 cm	4 to 10 cm
Achene:				
length	7 to 8 mm	6 to 7 mm	8 to 10 mm	8 to 10 mm
pappus	absent	absent	absent	present
Root:				
habit	deep tap-root	carrot-like tap-root	deep tap-root	deep tap-root
surface	rough	smooth	smooth	smooth
Caudex habit	multiple crown of erect branches	simple crown	multiple crown of erect branches	multiple-crown of erect branches



FIGS. 1-3. Meiotic chromosomes (diakinesis) in *Balsamorhiza*. 1 and 2, *B. hookeri* var. *hispidula*, $n = 20$ (\times ca 800); 3, *B. macrophylla*, $n = \text{ca } 100$ (\times ca 1080), multivalents indicated by arrows.

Morphological comparisons are provided in Table 2 for *B. sagittata* (sect. *Artorhiza*), *B. hookeri* var. *hispidula* (sect. *Balsamorhiza*), *B. macrophylla* and *W. amplexicaulis*. *Balsamorhiza macrophylla* is usually placed in section *Balsamorhiza* because of its pinnately dissected leaves. However, the root-caudex of *B. macrophylla* has characteristics intermediate between the two sections, viz., a large taproot with multiple crowns that produce rhizomes in immature plants.

Analysis of the morphological characters expressed in *B. sagittata*, *B. hookeri* var. *hispidula* and *B. macrophylla* indicates that the latter has features that are intermediate between the other two taxa. *Balsamorhiza macrophylla* is similar to *B. hookeri* var. *hispidula* in root habit, basal leaf shape, basal leaf margin, distribution of trichomes on the basal leaf surfaces, and trichome characteristics of the phyllaries (Table 2). The characters common to *B. macrophylla* and *B. sagittata* are the multiple-crowned caudex, shoot habit, length of root and shape of phyllary. However, *B. macrophylla* has some characters that are unknown in these or any other species of the genus, viz., glabrous stems and basal leaves (including the petiole base) and the large size of the stems, leaves, heads, phyllaries, and achenes. These characteristics do occur in *Wyethia*. *Balsamorhiza macrophylla* thus appears to combine characters of the two sections of the genus, and perhaps also of the genus *Wyethia*.

Geographic distribution and ecological requirements. There are some differences in the broad habitat requirements of the two sections of *Balsamorhiza* and only rarely do species of the two sections occur in close proximity. Species of section *Artorhiza* seem to prefer deep, well-drained,

often rocky but fairly fertile soils. In contrast, members of section *Balsamorhiza* mostly occupy shallow, sterile, rocky soil, primarily in xeric habitats. *Balsamorhiza macrophylla* and another meadow species, *B. incana*, are notable exceptions.

Balsamorhiza macrophylla is not widespread; it occurs in large populations in the lower and middle montane areas of northern Utah, southwestern Idaho, western Wyoming, and southwestern Montana. The ranges of *Balsamorhiza hookeri* and *B. sagittata* either widely overlap or interdigitate with that of *B. macrophylla* (fig. 4). *Balsamorhiza hookeri* var. *hispidula* is found in small populations throughout the Great Basin at relatively low elevations along the foothills of various mountain ranges. Populations of this species sometimes occur in close proximity to those of *B. macrophylla* along the western slopes of the Wasatch Mountains in north central Utah. *Balsamorhiza sagittata* is the most widely distributed species in the genus; its range overlaps the ranges of both the above-mentioned species and extends as far north as southern British Columbia, south to California, east to the Black Hills of South Dakota, and into western Colorado. In northern Utah, *B. sagittata* occurs primarily in lower montane regions where it is often close to populations of both *B. macrophylla* and *B. hookeri* var. *hispidula*.

Wyethia is confined to the western United States. Two species occur within the area of *B. macrophylla* (Weber, 1946), and one of these, *W. amplexicaulis*, is distributed in close proximity to the three species of *Balsamorhiza* mentioned above.

Ecological studies of foothill grasslands on the Wasatch Mountains present good evidence that *B. sagittata* and *B. macrophylla* belong to separate and distinct plant associations (Kleiner and Harper, 1966). *Balsamorhiza sagittata* is found primarily in a stable community containing equal percentages of annuals and perennials. By contrast, *B. macrophylla* favors a more disturbed habitat characterized by a higher percentage of annuals. Further investigation by Ludwig (1969) produced statistical evidence that *B. sagittata* and *B. macrophylla* also have different soil preferences. While *B. sagittata* occupies soils of high rock content, low percent clay, and comparatively low moisture content, *B. macrophylla* is found in soils of significantly lower rock content, high percent clay, and higher moisture content. Ludwig's analysis did not include *B. hookeri* var. *hispidula*, but observations made during the present study indicate that this species prefers sterile, rocky soils of low water content.

Balsamorhiza macrophylla also appears to have a level of frost tolerance higher than other species of the genus. During breeding experiments it was observed that both enclosed and exposed heads of *B. sagittata* plants were killed by late frost, while heads of adjacent plants of *B. macrophylla* were unaffected. Other parts of the plants of both species showed no apparent damage. It may be noted that *W. amplexicaulis* also has high frost tolerance (Weber, 1952). While *W. amplexicaulis* occurs

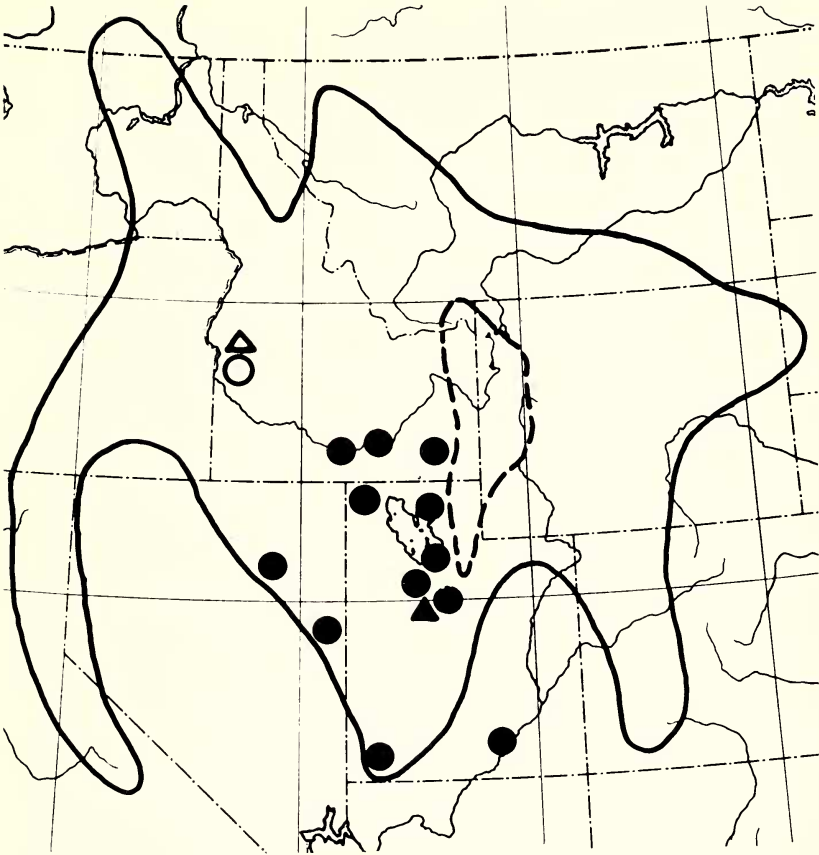


FIG. 4. Western United States, showing approximate distribution of four *Balsamorhiza* entities and putative hybrids. *B. sagittata*, solid line; *B. macrophylla*, dash line; *B. hookeri* var. *hispidula*, solid disk; *B. hookeri* var. *idahoensis*, open disk; *B. sagittata* × *hookeri* var. *hispidula*, solid triangle; *B. sagittata* × *hookeri* var. *idahoensis*, open triangle.

in a different plant association than either *B. sagittata* or *B. macrophylla*, its soil preferences with regard to percent of rock, clay, and water are almost identical to the soil preferences of *B. macrophylla* (Kleiner and Harper, 1966; Ludwig, 1969).

Hybridization in Balsamorhiza. Floral initiation in *Balsamorhiza* occurs at least four years after seedling establishment. Extended breeding tests have not been made, and observations on breeding have been made entirely in the field.

Several cases of natural hybridization in *Balsamorhiza* have been reported. Intersectional hybridization has been described by Maguire (1942), Ownbey and Weber (1943) and Stutz (in Drobnick and Plummer, 1966). Ownbey and Weber (1943) have drawn attention to the

curious situation that infrasectional isolation seems to be stronger than intersectional isolation, and discussed the phenomenon in relation to introgression and the origin of new taxa.

An analysis has been made of the recombination of some characters in a putative hybrid population between *B. sagittata* and *B. hookeri* var. *hispidula* found in Provo Canyon, Utah Co., Utah. The relationship between leaf base characters (sagittate in *B. sagittata* and acute in *B. hookeri* var. *hispidula*) and leaf margin characters (entire in *B. sagittata* and pinnately divided in *B. hookeri* var. *hispidula*) is approximately linear (fig. 5). The distribution is widely scattered on either side of the regression line, however, indicating a considerable amount of recombination. Field observations confirmed that putative hybrids more nearly resembling one parent generally occurred in close proximity to populations of that parental species. The approximately linear relationship between leaf base and leaf margin recorded in the above analysis, and the high frequency of individuals morphologically close to parental types suggest that backcrossing and introgression may be taking place.

Reciprocal crosses were attempted in the field, involving *B. sagittata*, *B. hookeri* var. *hispidula* and *B. macrophylla*. Inflorescence buds of these three species were also kept enclosed in cheesecloth covers for the duration of the flowering period. The only seeds obtained were from the crosses *B. sagittata* × *B. hookeri* var. *hispidula* (33 seeds) and *B. macrophylla* × *B. hookeri* var. *hispidula* (7 seeds). The seeds were planted in flats in the following fall. A low percentage of seeds of *B. sagittata* × *B. hookeri* var. *hispidula* germinated early in the next spring, but no seeds of the *B. macrophylla* × *B. hookeri* var. *hispidula* cross germinated. The seedlings were accidentally killed later in the season.

The results of the crossing program, being very limited, must be interpreted with caution. It may be suggested (1) that the species tested will cross in some combinations, and at least in one case produce viable seed, and (2) that the species are not self-pollinated (at least without the aid of a pollen vector). Apomixis is not likely to be involved.

There are no published accounts of natural hybridization involving *B. macrophylla*, nor of hybridization between *Balsamorhiza* and *Wyethia*.

GENERAL DISCUSSION

Balsamorhiza macrophylla appears to have an anomalous position with regard to the current taxonomy of the genus. It is intermediate between the two sections of the genus in its combination of morphological characters and in some aspects of its habitat requirements. The species also has some morphological and physiological characters that are unusual in *Balsamorhiza* but are present in the closely related genus *Wyethia*. The geographic distribution of the species is consistent with a putative hybrid origin from parental stocks in the two sections of *Balsamorhiza* and perhaps also in *Wyethia*.

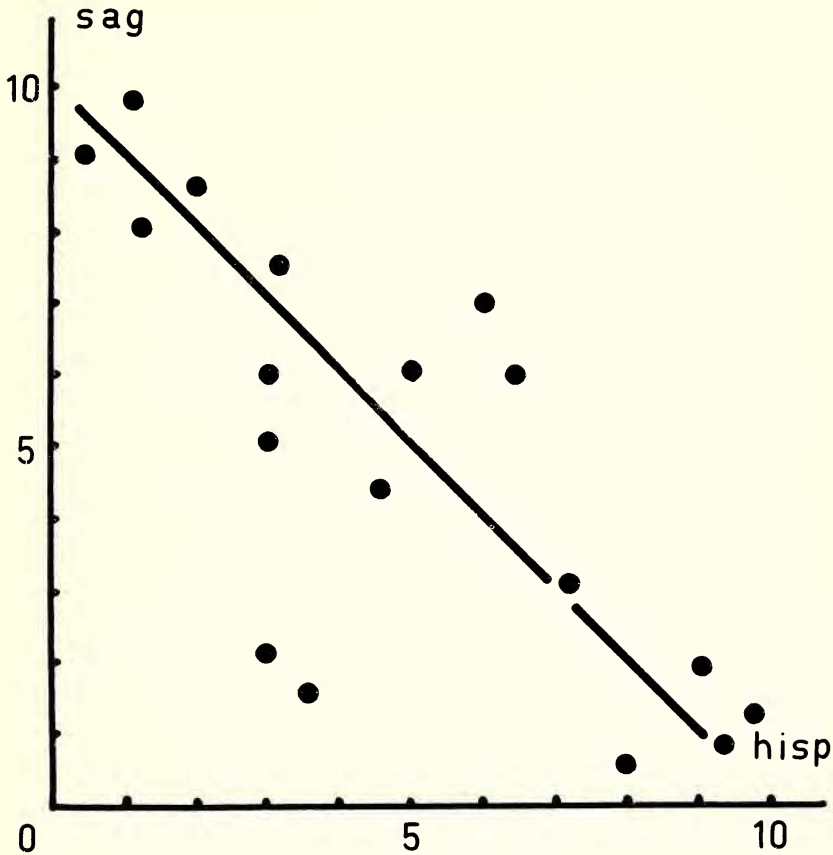


FIG. 5. Relationship between leaf base and leaf margin characters in a putative hybrid population between *B. sagittata* (sag) and *B. hookeri* var. *hispidula* (hisp). Character expression has been estimated on 10-point scales.

Intersectional hybridization in *Balsamorhiza* is well documented. It is clear from studies of segregation in putative hybrids between *B. sagittata* and *B. hookeri* var. *hispidula* that many characters of *B. macrophylla* may be derived from this parental combination, and they may reasonably be regarded as putative parents of the latter species. It is also possible, of course, that selection and adaptation in a hybrid population derived from these parents may also result in the establishment of characters that occur in neither parent. Thus, while some characters of *B. macrophylla*, such as glabrous stems and frost tolerance, may be taken subjectively to indicate involvement of *Wyethia* in the origin of *B. macrophylla*, there is no other evidence for this proposition, and these characters may also have been established following segregation and selection

in infrageneric hybrids. It is further possible that characters such as frost tolerance may be a consequence of polyploidy *per se* (Löve and Löve, 1957). Conversely *B. macrophylla* has no characters in common with *B. sagittata* that are not also expressed in *Wyethia amplexicaulis*, and an origin for *B. macrophylla* from a simple intergeneric cross could also be proposed. A more intensive morphological analysis is obviously required to clarify the relationships of the species.

Balsamorhiza macrophylla nevertheless appears to be a hybrid entity that has been fixed by polyploidy. The very high ploidy level involved, and the relatively high fertility of the diploid hybrids examined, indicate that the establishment of polyploidy has not been primarily in response to selection against partial sterility. The high ploidy level recorded must have been established in response to very strong selection for conservation of an adaptive genotype. This is borne out by the apparent uniformity of the entity.

An important requirement for further study is a detailed analysis of variation in *B. macrophylla* throughout its range, coupled with an intensive cytogeographic survey. It is important to determine the extent of the ca 10-ploid state, and whether any other ploidy levels exist in the species. It may be noted that the present chromosome count is from near the southern extremity of the distribution of the species. A search for other ploidy levels and an analysis of variation in this taxon will have an important bearing on our understanding of its age, origin, and taxonomic status.

CONCLUSIONS

Morphological, ecological, and cytological considerations suggest that *B. macrophylla* has had its origin through hybridization. The origin of the species may have been through a wide cross involving members of the two sections of *Balsamorhiza* and/or *Wyethia*, bringing together the vigorous, somewhat weedy nature of some taxa, the soil requirements of others, and such characters as frost tolerance. It is suggested that the new form was successful in disturbed habitats with deep soils at mid elevations in the Wasatch and similar mountain ranges. This adaptive biotype has been conserved by establishment of a high polyploid race. Further understanding of the origin of *B. macrophylla* requires an intensive morphological and cytogeographic analysis.

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NOTES AND NEWS

HAPLOPAPPUS LYALLII GRAY (COMPOSITAE), A NEW RECORD FROM CALIFORNIA.—*Haplopappus lyallii* Gray is a caespitose perennial found in alpine habitats between elevations of 5,500 and 11,000 feet in the northwestern U.S. and British Columbia. On August 11, 1970, I collected this species in northern Trinity Co., Calif. (T36N, R11W, Sec. 12; *Ferlatte & Howard 1308*: HSC, UC), approximately 230 miles from its nearest known localities in the Blue Mts. of Baker Co., Oregon, and the mountains of northeast Nevada (Hitchcock, C. L., et al. 1955. *Vascular Plants of the Pacific Northwest. Part 5: Compositae*, by Arthur Cronquist, Univ. of Wash. Press, Seattle, p. 220.). There are approximately two dozen plants growing in dry, decomposed granite at an elevation of 8,800 feet on the west ridge of Thompson Pk. *Haplopappus lyallii* has also been collected about one mile to the south on the crest between Canyon Cr. and the Rattlesnake Cr. drainage (T36N, R11W, Sec. 13; *J. O. Sawyer 2337*: HSC, July 22, 1970). Associated species include the following: *Hieracium gracile* Hook., *Draba howellii* Wats., *Lupinus lobbii* Gray ex Greene, and *Pinus albicaulis* Englem.—WILLIAM J. FERLATTE, California Department of Agriculture, Sacramento 95823.

MALACOTHRIX TORREYI (COMPOSITAE) IN CALIFORNIA.—Apparently *Malacothrix torreyi* Gray has been collected in California on only one or two occasions. One collection was made by Annie M. Alexander and Louise Kellogg on June 4, 1946, "seven miles east of Eagleville, Modoc Co., elevation 5150 feet" (UC). However, the state line is exactly six miles east of Eagleville, though undoubtedly unmarked or poorly marked in this area, and it is likely that this collection is actually from Nevada. A second and slightly less equivocal record of this species in California was made on July 2, 1967, on disturbed gravelly soils derived from basaltic rock at about 8500 feet just north of Masonic Peak in Mono Co. (*Hardham 15084*, CAS). The two dominant species at this site, *Pinus monophylla* and *Artemisia tridentata*, were of scattered occurrence and associated species were infrequent. The *Malacothrix* occurred on the upper margins of the pinyon community and was not observed at lower elevations.—CLARE B. HARDHAM, Creston Star Route, Paso Robles, California 93446, and GORDON H. TRUE, JR., 142 Margarita Drive, San Rafael, California 94901.